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Effects of Fire on Nutrient Concentrations and Standing Crops in Biomass of *Juncus roemerianus* and *Spartina bakeri* Marshes

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ABSTRACT

We examined effects of fire on nutrient concentrations and standing crops in *Juncus roemerianus* and *Spartina bakeri* marshes by sampling biomass from 25 plots (0.25 m^2) in each marsh before and one year after a fire, separating samples by taxon and live or standing dead categories, and analyzing for total Kjeldahl nitrogen (TKN), P, K, Ca, and Mg. Nitrogen concentrations were lower in all biomass types one year after burning. Phosphorus concentrations increased in live *Spartina*, decreased in live *Juncus* and live *Sagittaria* in the *Juncus* marsh, and were unchanged in other types; however, the ratio of P to N increased in all live biomass types. Concentrations of K declined or remained unchanged. Calcium concentrations increased in *Juncus* and *Spartina*. Magnesium concentrations decreased in live and dead *Juncus* (*Juncus* marsh), but increased in live *Sagittaria* (*Juncus* marsh), dead *Sagittaria* (*Spartina* marsh), and live *Spartina*. Live biomass generally had higher concentrations of N, P, and K but lower levels of Ca than dead biomass. Standing crops of all nutrients were much lower than one year after fire than preburn. Our results differ from the increases in many tissue nutrients recorded soon after fire in other studies. Nutrient concentrations often decline with tissue age; thus, concentrations one year postburn may have differed from those immediately postburn. The absence of an increase in available soil N until six months postburn may have limited N concentrations in regrowing biomass. Standing crops of biomass and nutrients did not reestablish preburn levels in these marshes in one year.

INTRODUCTION

Fires occur naturally in many wetlands (Kirby et al. 1988). In the southeastern United States these include cypress and hardwood swamps (e.g., Cypert 1961, Izlar 1984, Hermann et al. 1991, Cook and Ewell 1992), pocosin shrublands (e.g., Christensen et al. 1981, Wilbur and Christensen 1983), and various marshes (e.g., Penfound and Hathaway 1938, Vogl 1973, Wade et al. 1980, Duever et al. 1986, Davison and Bratton 1988). Prescribed burning is used in marsh management for purposes that include reducing shrub invasion of graminoid wetlands (Kushland 1990, Huffman and Blanchard 1991, Wade 1991), improving grazing (McAtee et al. 1979b), and encouraging growth of preferred wildlife food (Givens 1962, Goodwin 1979).

Fire is a major mineralizing factor in many ecosystems. Fire releases nutrients from live and dead biomass to the atmosphere as gases or particulates (e.g., Raison et al. 1985a, 1985b; Cofer et al. 1988a, 1988b, 1989, 1990a, 1990b; Crutzen and Andreae 1990) or to the soil surface as ash and partially burned residue (e.g., Raison 1979, Wells et al. 1979, Rundel 1981). Fire may strongly influence nutrient cycling on local (e.g., Boerner and Forman 1982) or regional (e.g., Robertson and Rosswall 1986) scales. One important factor in determining fire effects on nutrient cycling is the standing crops of nutrients in a system before burning and the rates at which these recover after fire (e.g., Boerner 1982, Kellman et al. 1987).

Fire occurs in many grasslands (e.g., Daubenmire 1968, Wright and Bailey 1982, Collins and Wallace 1990). Frequently, short-term increases (persisting a few months) in nutrient concentrations in regrowing biomass occur (Daubenmire 1968). Longer-term trends may differ. Christensen (1977) found increased N, P, K, Ca, and Mg in leaf tissue of *Aristida stricta* Michaux for two to three months after burning of a pine-wiregrass savanna. At one year after fire, N and P were lower, and K, Ca, and Mg were equal or less than in the unburned stand. Two growing seasons after fire, Wein and Bliss (1973) found increased tissue concentrations (particularly N, P, K) for some species in tussock tundra. Ohr and Bragg (1985) found increased P, K, and Zn, and decreased Ca and Mg in several tallgrass prairie species; some changes persisted as long as three years after a single fire. Fire frequency and recency affected nutrient concentrations, and some patterns differed between species (Ohr and Bragg 1985). Increased tissue concentrations do not always occur. Koelling and Kucera (1965) found lower tissue levels of N and K in burned than in unburned tallgrass prairie through one year postfire that they attributed to more rapid growth and greater production in the burned prairie.

Christensen (1977) noted the importance of tissue age in determining nutrient concentrations; P and K concentrations were the same in burned and clipped sites (tissue age equal), while N, Ca, and Mg were higher in burned than clipped plots. Newly emerged shoots of *Carex* spp. had the highest concentrations of many nutrients (N, P, K) which declined as the shoots aged (Bernard and Solsky 1977, Auclair 1982, Bernard et al. 1988).

Although fire occurs in many marshes (Kirby et al. 1988), few data are available on fire effects on marsh biomass chemistry. Steward and Ornes (1975) found high concentrations of N, P, K, Mg, Mn, and Cu in regrowing Everglades sawgrass (*Cladium jamaicense* Crantz) marsh that decreased by three to five months after fire, while Ca and Fe increased over time. Auclair (1977) found a negative correlation between fire incidence and tissue nutrient concentrations in *Carex* meadows in southern Quebec. Concentrations of many nutrients increased one to two months after burning of *Juncus roemerianus* Scheele and *Spartina cynosuroides* (L.) Roth marshes in coastal Mississippi (Faulkner and de la Cruz 1982). Hackney and de la Cruz (1983) reported increased N concentrations that persisted about two months after a winter burn in a *Juncus roemerianus* marsh but cutting produced a similar N increase. McAtee et al. (1979a) and Angell et al. (1986) found increased crude protein (crude protein = 6.25 × total N, Heath et al. 1973) for one to three months after burning of *Spartina spartinae* (Trin.)

Merr. ex Hitchc. coastal prairie in Texas. Smith et al. (1984) found increased crude protein in spring regrowth of *Distichlis spicata* (L.) Greene, *Scirpus lacustris* L., and *Typha* spp. after a fall burn in a Great Salt Lake marsh; decreased crude protein in *Scirpus maritimus* L. was attributed to intense grazing. Smith (1989) found no differences in crude protein in regrowing cattail (*Typha latifolia* L.) in burned and unburned Texas playa marshes.

In this paper we examine the concentrations and standing crops of major nutrients in biomass of *Juncus roemerianus* and *Spartina bakeri* Merr. marshes before and one year after a fire to determine if increases in tissue nutrient concentrations occur one year after burning and if preburn biomass nutrient pools recover by this time. Since prescribed burning is used to manage these marshes along with water level manipulation, it is important to begin to understand the impacts of fire on standing crop biomass nutrient pools and the patterns of recovery with time. We have previously reported on changes in species composition and biomass (Schmalzer et al. 1991b) and soils (Schmalzer et al. 1991a, Schmalzer and Hinkle 1992) following fire in these marshes. In these studies, we found that species composition and dominance of *Juncus* and *Spartina* marshes one year after burning were similar to that of preburn, but biomass did not recover as rapidly. In the *Juncus* marsh one year after burning, live biomass was 47.2%, standing dead 18.7%, and total biomass 29.3% of that before burning. In the *Spartina* marsh, biomass one year after burning was live 42.3%, standing dead 21.4%, and total 30.7% of that before burning (Schmalzer et al. 1991b). Soil parameters showed differing patterns of change after burning. Soil pH increased immediately postburn but returned to preburn levels in one month. Calcium, Mg, K, and PO_4-P increased one month postburn, and the increases persisted through six (K, PO_4-P) to 12 (Ca, Mg) months postburn. Nitrogen species were affected by seasonally varying water levels as well as fire; in burned marshes, NH_4-N was elevated six months and NO_3-N 12 months after fire (Schmalzer and Hinkle 1992).

METHODS

Study Site

This study was conducted at John F. Kennedy Space Center (KSC) located on Merritt Island on the east coast of central Florida. KSC consists of 57,000 ha of land and open water lagoons. Areas not actively used by the space program are managed as Merritt Island National Wildlife Refuge (MINWR) by the U.S. Fish and Wildlife Service (USFWS) or by the National Park Service as Canaveral National Seashore. Prescribed burning of uplands and wetlands on MINWR is conducted by the USFWS as part of their management program (Lee et al. 1981). See Schmalzer et al. (1991b) for a more complete description of the area.

The site for the specific study was a 2,006 ha controlled burn unit previously burned in December 1985. With the fire management unit, we selected two representative marshes scheduled to be burned, one dominated by *Juncus roemerianus* and one by *Spartina bakeri*. At the time of the site selection (Sept 1988), both marshes were flooded to a similar depth (ca. 15–30 cm). Both marshes were burned on 11 November 1988 by USFWS/MINWR personnel. Seasonal water level fluctuations occurred with precipitation and evapotranspiration. Marshes remained flooded through three months postburn (Feb); water levels receded below the surface six months postfire (May), remained unflooded nine months postburn (Aug), but reflooded 12 months after the fire.

Biomass Sampling and Analysis

In September 1988, one month before the fire, we sampled above-ground biomass of the *Juncus* and *Spartina* marshes by harvesting 25 randomly selected plots (0.25 m^2) in each marsh. Sample size was determined using data from a pilot study in 1987 and the sample size criteria of Green (1979). One year after burning (Nov 1989), we repeated the sampling; samples were taken randomly within areas of the marshes that had burned. Biomass samples were separated by taxa and by live and dead categories, weighed, oven-dried at 100°C for 24 hours, and dry weights determined. Dried samples were ground in a Wiley mill. For cations and phosphorus, 1 g of oven-dried material was dry ashed at 450°C in a muffle furnace and taken up in hydrochloric acid. Analyses for Ca, Mg, and K were performed on an inductively coupled plasma spectrometer (Wallace and Barrett 1981). Total P was determined on an autoanalyzer (Technicon Industrial Systems 1983b). Total Kjeldahl nitrogen (TKN) was determined by digesting a 0.25 g sample in 2 ml concentrated H_2SO_4, 2 ml 30% H_2O_2, and 4 ml of K_2SO_4 digestion mixture in a model BD-40 block digester and analyzing on an autoanalyzer (Technicon Industrial Systems 1983a). Standing crops of Ca, Mg, K, P, and TKN were calculated by multiplying the amount of each biomass category for a plot by its respective concentration.

Nutrient concentrations and standing crops from preburn to one year postburn samples within the same marsh were compared by taxa, and live or standing dead categories to reduce variability. Concentrations were not all normally distributed ($p < 0.05$, Kolmogorov-Smirnov test, SPSS Inc. 1988); therefore, we used the nonparametric, Mann-Whitney U test (SPSS Inc. 1988) for these comparisons.

RESULTS

Nutrient Concentrations

Nitrogen concentrations in all biomass types were substantially lower one year after burning than preburn (Table 1). Phosphorus concentrations in live *Juncus* and live *Sagittaria* in the *Juncus* marsh decreased, concentrations increased in live *Spartina* in the *Spartina* marsh, and other concentrations did not change significantly (Table 2). However, the ratio of P to N increased in all live biomass categories from preburn to one year postburn. In live *Juncus,* P to N ratios increased from 1:12.2 to 1:8.5 in the *Juncus* marsh and from 1:18.8 to 1:9.4 in the *Spartina* marsh. In live *Sagittaria,* P to N ratios increased from 1:9.9 to 1:6.3 in the *Juncus* marsh and from 1:16.4 to 1:7.4 in the *Spartina* marsh. In live *Spartina,* the P to N ratio increased from 1:16.9 to 1:6.0. Potassium concentrations generally declined or did not change significantly (Table 3). Calcium concentrations increased in live *Juncus* (both marshes), live *Spartina,* dead *Juncus* (*Juncus* marsh), dead *Sagittaria* (*Juncus* marsh), and dead *Spartina*

Table 1. Total Kjeldahl nitrogen concentrations and standing crops before and one year after burning. Data are means with standard deviations in parentheses. Data from minor species are not given but are included in total standing crops

	Concentrations				Standing Crops			
	Juncus Marsh		*Spartina* Marsh		*Juncus* Marsh		*Spartina* Marsh	
Biomass Type	Preburn (mg/kg)	1 Year Postburn (mg/kg)	Preburn (mg/kg)	1 Year Postburn (mg/kg)	Preburn (g/m²) N = 25	1 Year Postburn (g/m²) N = 25	Preburn (g/m²) N = 25	1 Year Postburn (g/m²) N = 25
Live *Juncus roemerianus*	7,304.2	3,917.2[c]	8,433.0	3,240.8[b]	5.047	1.218[c]	0.137	0.185[a]
	(985.8)	(501.8)	(3,175.6)	(649.7)	(1.673)	(0.400)	(0.364)	(0.184)
	N = 25	N = 25	N = 4	N = 18				
Dead *Juncus roemerianus*	5,379.6	2,420.0[c]	4,406.0	2,023.9[a]	4.842	0.359[c]	0.276	0.098[a]
	(1,278.7)	(376.5)	(629.1)	(1,178.8)	(2.281)	(0.098)	(0.955)	(0.250)
	N = 25	N = 25	N = 3	N = 13				
Live *Sagittaria lancifolia*	15,147.0	6,948.5[c]	17,260.4	7,110.7[c]	1.749	0.206[c]	1.926	0.073[c]
	(2,671.6)	(948.1)	(1,960.5)	(1,098.9)	(0.807)	(0.098)	(0.914)	(0.059)
	N = 25	N = 25	N = 24	N = 20				
Dead *Sagittaria lancifolia*	10,606.2	4,196.2[c]	12,957.4	5,131.4[c]	1.220	0.142[c]	2.495	0.126[c]
	(1,437.3)	(797.1)	(2,147.8)	(988.7)	(0.621)	(0.082)	(2.592)	(0.110)
	N = 25	N = 25	N = 24	N = 23				

Table 1. Continued

Biomass Type	Concentrations				Standing Crops			
	Juncus Marsh		*Spartina* Marsh		*Juncus* Marsh		*Spartina* Marsh	
	Preburn (mg/kg)	1 Year Postburn (mg/kg)	Preburn (mg/kg)	1 Year Postburn (mg/kg)	Preburn (g/m^2) N = 25	1 Year Postburn (g/m^2) N = 25	Preburn (g/m^2) N = 25	1 Year Postburn (g/m^2) N = 25
Live *Spartina bakeri*	—	—	2,957.3 (982.7) N = 24	1,787.6[c] (470.4) N = 25	—	—	1.822 (1.452)	0.422[c] (0.202)
Dead *Spartina bakeri*	—	—	3,860.4 (975.0) N = 24	1,431.0[c] (309.9) N = 24	—	—	2.873 (1.697)	0.203[c] (0.108)
Total live					6.859 (1.804)	1.438[c] (0.410)	4.595 (1.874)	0.692[c] (0.272)
Total dead					6.062 (2.575)	0.501[c] (0.129)	5.645 (3.109)	0.427[c] (0.238)
Total					12.921 (3.933)	1.939[c] (0.449)	10.240 (4.753)	1.119[c] (0.419)

Differences based on Mann-Whitney U test between preburn and 1 year postburn concentrations or standing crops within each marsh

[a] $p \leq 0.05$

[b] $p \leq 0.01$

[c] $p \leq 0.001$

Table 2. Phosphorus concentration and standing crops before and one year after burning. Data are means with standard deviations in parentheses. Data from minor species are not given but are included in total standing crops

	Concentrations				Standing Crops			
	Juncus Marsh		*Spartina* Marsh		*Juncus* Marsh		*Spartina* Marsh	
Biomass Type	**Preburn (mg/kg)**	**1 Year Postburn (mg/kg)**	**Preburn (mg/kg)**	**1 Year Postburn (mg/kg)**	**Preburn (g/m²) N = 25**	**1 Year Postburn (g/m²) N = 25**	**Preburn (g/m²) N = 25**	**1 Year Postburn (g/m²) N = 25**
Live *Juncus roemerianus*	598.0	461.4[c]	447.5	346.2	0.416	0.141[c]	0.008	0.021
	(157.5)	(118.0)	(180.3)	(83.4)	(0.182)	(0.050)	(0.023)	(0.022)
	N = 25	N = 25	N = 4	N = 18				
Dead *Juncus roemerianus*	335.0	225.2	100.0	121.1	0.296	0.033[c]	0.007	0.006[a]
	(312.6)	(87.7)	(36.1)	(51.4)	(0.305)	(0.014)	(0.026)	(0.013)
	N = 25	N = 25	N = 3	N = 13				
Live *Sagittaria lancifolia*	1,533.6	1,099.4[c]	1,053.1	959.6	0.181	0.033[c]	0.120	0.010[c]
	(328.8)	(310.6)	(184.6)	(369.4)	(0.093)	(0.018)	(0.065)	(0.009)
	N = 25	N = 24	N = 24	N = 20				
Dead *Sagittaria lancifolia*	383.0	265.2[c]	238.4	295.8	0.045	0.009[c]	0.044	0.007[c]
	(109.1)	(67.1)	(65.4)	(187.7)	(0.027)	(0.005)	(0.045)	(0.007)
	N = 25	N = 25	N = 25	N = 23				
Live *Spartina bakeri*	—	—	175.4	296.4[c]	—	—	0.100	0.067[a]
			(77.5)	(253.1)			(0.059)	(0.046)
			N = 24	N = 25				

Table 2. Continued

Biomass Type	Concentrations: *Juncus* Marsh Preburn (mg/kg)	Concentrations: *Juncus* Marsh 1 Year Postburn (mg/kg)	Concentrations: *Spartina* Marsh Preburn (mg/kg)	Concentrations: *Spartina* Marsh 1 Year Postburn (mg/kg)	Standing Crops: *Juncus* Marsh Preburn (g/m^2) N = 25	Standing Crops: *Juncus* Marsh 1 Year Postburn (g/m^2) N = 25	Standing Crops: *Spartina* Marsh Preburn (g/m^2) N = 25	Standing Crops: *Spartina* Marsh 1 Year Postburn (g/m^2) N = 25
Dead *Spartina bakeri*	—	—	113.5 (55.3) N = 24	99.3 (34.3) N = 24	—	—	0.083 (0.057)	0.013[c] (0.006)
Total live					0.603 (0.210)	0.176[c] (0.047)	0.247 (0.072)	0.099[c] (0.052)
Total dead					0.341 (0.313)	0.042[c] (0.015)	0.134 (0.065)	0.026[c] (0.014)
Total					0.943 (0.400)	0.218[c] (0.054)	0.381 (0.112)	0.125[c] (0.060)

Differences based on Mann-Whitney U test between preburn and 1 year postburn concentrations or standing crops within each marsh

[a] $p \leq 0.05$

[b] $p \leq 0.01$

[c] $p \leq 0.001$

Table 3. Potassium concentration and standing crops before and one year after burning. Data are means with standard deviations in parentheses. Data from minor species are not given but are included in total standing crops

Biomass Type	Concentrations				Standing Crops			
	Juncus Marsh		*Spartina* Marsh		*Juncus* Marsh		*Spartina* Marsh	
	Preburn (mg/kg)	1 Year Postburn (mg/kg)	Preburn (mg/kg)	1 Year Postburn (mg/kg)	Preburn (g/m^2) N = 25	1 year Postburn (g/m^2) N = 25	Preburn (g/m^2) N = 25	1 Year Postburn (g/m^2) N = 25
Live *Juncus roemerianus*	5,466.3	4,324.8[b]	6,771.5	4,630.3	3.795	1.366[c]	0.145	0.265
	(2,010.4)	(875.2)	(2,030.9)	(1,503.5)	(1.841)	(0.537)	(0.409)	(0.260)
	N = 25	N = 25	N = 4	N = 18				
Dead *Juncus roemerianus*	997.2	552.7[c]	1,245.3	340.2[a]	0.890	0.080[c]	0.094	0.023[a]
	(388.3)	(1,472.9)	(692.6)	(493.6)	(0.448)	(0.200)	(0.374)	(0.079)
	N = 25	N = 25	N = 3	N = 13				
Live *Sagittaria lancifolia*	33,451.7	24,705.8[c]	33,028.4	22,216.9[c]	3.818	0.746[c]	3.728	0.234[c]
	(6,416.8)	(6,738.4)	(4,002.3)	(10,894.7)	(1.666)	(0.416)	(1.892)	(0.247)
	N = 25	N = 24	N = 24	N = 20				
Dead *Sagittaria lancifolia*	2,824.1	834.3[c]	1,983.4	2,012.5[c]	0.301	0.030[c]	0.346	0.038[c]
	(1,143.8)	(322.4)	(824.0)	(4,690.2)	(0.148)	(0.024)	(0.327)	(0.090)
	N = 25	N = 25	N = 25	N = 23				
Live *Spartina bakeri*	—	—	3,154.8	4,375.9	—	—	1.874	0.999[c]
			(750.2)	(6,552.2)			(1.196)	(1.109)
			N = 24	N = 25				

Table 3. Continued

	Concentrations				Standing Crops			
	Juncus Marsh		*Spartina* Marsh		*Juncus* Marsh		*Spartina* Marsh	
Biomass Type	**Preburn (mg/kg)**	**1 Year Postburn (mg/kg)**	**Preburn (mg/kg)**	**1 Year Postburn (mg/kg)**	**Preburn (g/m^2) N = 25**	**1 year Postburn (g/m^2) N = 25**	**Preburn (g/m^2) N = 25**	**1 Year Postburn (g/m^2) N = 25**
Dead *Spartina bakeri*	—	—	596.2	233.3[c]	—	—	0.420	0.034[c]
			(238.8)	(130.0)			(0.266)	(0.029)
			N = 24	N = 24				
Total live					7.666	2.134[c]	6.212	1.519[c]
					(1.945)	(0.550)	(1.989)	(1.166)
Total dead					1.191	0.109[c]	0.860	0.096[c]
					(0.491)	(0.200)	(0.496)	(0.112)
Total					8.858	2.244[c]	7.072	1.615[c]
					(2.151)	(0.580)	(2.264)	(1.165)

Differences based on Mann-Whitney U test between preburn and 1 year postburn concentrations or standing crops within each marsh

[a] $p \leq 0.05$
[b] $p \leq 0.01$
[c] $p \leq 0.001$

Table 4. Potassium concentration and standing crops before and one year after burning. Data are means with standard deviations in parentheses. Data from minor species are not given but are included in total standing crops

	Concentrations				Standing Crops			
	Juncus Marsh		*Spartina* Marsh		*Juncus* Marsh		*Spartina* Marsh	
Biomass Type	Preburn (mg/kg)	1 Year Postburn (mg/kg)	Preburn (mg/kg)	1 Year Postburn (mg/kg)	Preburn (g/m²) N = 25	1 Year Postburn (g/m²) N = 25	Preburn (g/m²) N = 25	1 Year Postburn (g/m²) N = 25
Live *Juncus roemerianus*	561.3	1,146.2[c]	724.8	1,285.6[b]	0.389	0.364	0.013	0.081
	(201.2)	(316.2)	(153.0)	(336.0)	(0.191)	(0.163)	(0.033)	(0.094)
	N = 25	N = 25	N = 4	N = 18				
Dead *Juncus roemerianus*	1,710.0	2,038.0[b]	1,320.0	1,616.5	1.498	0.311[c]	0.095	0.066[a]
	(564.1)	(464.0)	(572.1)	(555.8)	(0.697)	(0.126)	(0.358)	(0.127)
	N = 25	N = 25	N = 3	N = 13				
Live *Sagittaria lancifolia*	5,168.8	5,016.6	4,857.9	5,192.1	0.595	0.149[c]	0.548	0.048[c]
	(800.7)	(1,311.0)	(785.0)	(2,893.7)	(0.255)	(0.078)	(0.275)	(0.036)
	N = 25	N = 24	N = 24	N = 20				
Dead *Sagittaria lancifolia*	8,137.3	10,109.6[c]	8,192.3	8,396.3	0.909	0.325[c]	1.495	0.211[c]
	(1,621.8)	(1,991.3)	(1,318.3)	(2,089.9)	(0.473)	(0.158)	(1.272)	(0.191)
	N = 25	N = 25	N = 25	N = 23				
Live *Spartina bakeri*	—	—	643.5	1,344.4[c]	—	—	0.381	0.281[a]
			(149.4)	(1,637.8)			(0.233)	(0.259)
			N = 24	N = 25				

Table 4. Continued

	Concentrations				Standing Crops			
	Juncus Marsh		*Spartina* Marsh		*Juncus* Marsh		*Spartina* Marsh	
Biomass Type	**Preburn (mg/kg)**	**1 Year Postburn (mg/kg)**	**Preburn (mg/kg)**	**1 Year Postburn (mg/kg)**	**Preburn (g/m²) N = 25**	**1 Year Postburn (g/m²) N = 25**	**Preburn (g/m²) N = 25**	**1 Year Postburn (g/m²) N = 25**
Dead *Spartina bakeri*	—	—	937.3 (305.6) N = 24	1,388.7[c] (396.2) N = 24	—	—	0.658 (0.344)	0.185[c] (0.095)
Total live					1.064 (0.434)	0.527[c] (0.175)	1.054 (0.327)	0.426[c] (0.323)
Total dead					2.407 (0.795)	0.636[c] (0.170)	2.248 (1.286)	0.462[c] (0.209)
Total					3.471 (1.048)	1.163[c] (0.281)	3.302 (1.486)	0.888[c] (0.402)

Differences based on Mann-Whitney U test between preburn and 1 year postburn concentrations or standing crops within each marsh
[a] $p \le 0.05$
[b] $p \le 0.01$
[c] $p \le 0.001$

Table 5. Magnesium concentration and standing crops before and one year after burning. Data are means with standard deviations in parentheses. Data from minor species are not given but are included in total standing crops

	Concentrations				Standing Crops			
	Juncus Marsh		*Spartina* Marsh		*Juncus* Marsh		*Spartina* Marsh	
Biomass Type	Preburn (mg/kg)	1 Year Postburn (mg/kg)	Preburn (mg/kg)	1 Year Postburn (mg/kg)	Preburn (g/m²) N = 25	1 Year Postburn (g/m²) N = 25	Preburn (g/m²) N = 25	1 Year Postburn (g/m²) N = 25
Live *Juncus roemerianus*	518.5 (70.6) N = 25	421.1[c] (133.0) N = 25	614.8 (71.2) N = 4	511.4 (196.0) N = 18	0.360 (0.129)	0.132[c] (0.056)	0.012 (0.033)	0.029 (0.030)
Dead *Juncus roemerianus*	523.6 (144.0) N = 25	414.0[b] (126.5) N = 25	341.0 (74.1) N = 3	220.4 (133.9) N = 13	0.463 (0.208)	0.064[c] (0.029)	0.022 (0.079)	0.010[a] (0.020)
Live *Sagittaria lancifolia*	2,637.6 (403.5) N = 25	3,102.7[b] (937.9) N = 24	2,192.2 (259.9) N = 24	2,592.7 (850.1) N = 20	0.298 (0.119)	0.092[c] (0.047)	0.246 (0.118)	0.026[c] (0.020)
Dead *Sagittaria lancifolia*	2,173.6 (453.8) N = 25	2,372.6 (522.3) N = 25	1,775.9 (264.3) N = 25	2,165.6[a] (767.9) N = 23	0.239 (0.119)	0.079[c] (0.049)	0.327 (0.283)	0.051[c] (0.042)

Table 5. Continued

	Concentrations				Standing Crops			
	Juncus Marsh		*Spartina* Marsh		*Juncus* Marsh		*Spartina* Marsh	
Biomass Type	**Preburn (mg/kg)**	**1 Year Postburn (mg/kg)**	**Preburn (mg/kg)**	**1 Year Postburn (mg/kg)**	**Preburn (g/m^2) N = 25**	**1 Year Postburn (g/m^2) N = 25**	**Preburn (g/m^2) N = 25**	**1 Year Postburn (g/m^2) N = 25**
Live *Spartina bakeri*	—	—	298.2 (43.9) N = 24	738.9[c] (477.0) N = 25	—	—	0.176 (0.107)	0.161 (0.088)
Dead *Spartina bakeri*	—	—	254.2 (85.6) N = 24	359.7 (217.2) N = 24	—	—	0.178 (0.093)	0.043[c] (0.027)
Total live					0.675 (0.165)	0.232[c] (0.063)	0.468 (0.125)	0.221[c] (0.097)
Total dead					0.702 (0.235)	0.143[c] (0.050)	0.527 (0.288)	0.105[c] (0.046)
Total					1.377 (0.354)	0.375[c] (0.085)	0.995 (0.379)	0.325[c] (0.103)

Differences based on Mann-Whitney U test between preburn and 1 year postburn concentrations or standing crops within each marsh

[a] $p \leq 0.05$

[b] $p \leq 0.01$

[c] $p \leq 0.001$

(Table 4). Magnesium concentrations decreased in live and dead *Juncus* (*Juncus* marsh), but increased in live *Sagittaria* (*Juncus* marsh), dead *Sagittaria* (*Spartina* marsh), and live *Spartina* (Table 5). The ratio of Mg to Ca in live *Juncus* decreased from 1:1.08 to 1:2.72 in the *Juncus* marsh and from 1:1.18 to 1:2.51 in the *Spartina* marsh, consistent with the increased Ca levels but decreased or unchanged Mg. In live *Sagittaria,* the ratio of Mg to Ca increased from 1:1.96 to 1:1.62 in the *Juncus* marsh and from 1:2.22 to 1:2.00 in the *Spartina* marsh; in live *Spartina,* the increase was from 1:2.16 to 1:1.82, indicating that the increases in Mg in these species were greater relative to the increases in Ca.

In addition to differences associated with time since fire, differences due to biomass type (live or dead) and taxon were evident. In most cases, live biomass had higher concentrations of N (Table 1), P (Table 2), and K (Table 3) but lower levels of Ca (Table 4) than dead biomass. Differences in Mg (Table 5) were less consistent. Live *Sagittaria* had much higher concentrations of all nutrients than live *Juncus* or *Spartina*.

Nutrient Standing Crops

Total N standing crops and those of most biomass categories (Table 1) were much lower one year postburn than before burning. Before the fire, live and dead biomass N pools were about equal in the *Juncus* marsh, but dead exceeded live in the *Spartina* marsh. One year after fire, the live biomass pools exceeded dead in both marshes. Standing crops of P were much reduced one year after burning (Table 2). Live biomass was more important than dead both before and one year after fire. Potassium standing crops were reduced one year postburn (Table 3); the live biomass pool was more important than dead both before and after fire. Even though Ca concentrations increased after fire, standing crops decreased (Table 4). Before burning, the Ca pool in dead biomass was much larger than in live; one year postburn it was slightly larger. Magnesium standing crops were lower one year postburn (Table 5). Before burning, the Mg pool in standing dead slightly exceeded live, but one year postburn live exceeded dead.

DISCUSSION

Nutrient Concentrations

The reduced tissue N levels one year after fire differ from the short term increases reported for several marshes (Steward and Ornes 1975, McAtee et al. 1979a, Faulkner and de la Cruz 1982, Smith et al. 1984) but are similar to lower N levels one year after fire in some grasslands (Koelling and Kucera 1965) and savannas (Christensen 1977). If regrowth immediately after fire in these marshes had elevated N levels, by one year postburn they had declined. Decreased N concentrations in *Juncus roemerianus* (Gallagher et al. 1980) and *Spartina alterniflora* (Ornes and Kaplan 1989) have been attributed to rapid growth. Despite the decreased tissue N concentrations, there were no indications of N deficiency in the regrowing plants. Eleuterius and Caldwell (1981) found that *Juncus roemerianus* was more sensitive to deficiencies of Mg than of N. Available N (NH_4-N or NO_3-N) in the soil did not increase immediately after fire; NH_4-N was elevated in soils of the burned marshes six months and NO_3-N 12 months postburn

(Schmalzer and Hinkle 1992). The absence of a flush of available N soon after fire may have limited N concentrations in regrowing tissue.

Available P increased in soils of both burned marshes (Schmalzer and Hinkle 1992). Species differed in their responses, with concentrations declining in *Juncus* and *Sagittaria* and increasing in *Spartina*. As with N, short-term increases may have occurred (e.g., Steward and Ornes 1975, Faulkner and de la Cruz 1982), but biomass was not sampled at those times, and concentrations may have been reduced by subsequent growth as in *Cladium* (Steward and Ornes 1975) and *Aristida* (Christensen 1977). However, the increased ratio of P to N in all live biomass suggests greater availability of P relative to N after fire.

Potassium increased in soils of both burned marshes between one and six months after fire (Schmalzer and Hinkle 1992). Lower levels in tissues of some species one year after fire might be due to rapid growth. Potassium in *Cladium* tissue declined from initially high levels immediately after fire to lower levels in several months (Steward and Ornes 1975).

Calcium increased in soils of both burned marshes after fire (Schmalzer and Hinkle 1992). The increases in *Juncus* and *Spartina* tissue concentrations apparently relate to greater availability and may represent "luxury" consumption in excess of physiological requirements (Epstein 1972). Unlike N, P, and K, much of the Ca in plants is bound in structural material and is not readily retranslocated (Epstein 1972, Marschner 1986). *Sagittaria,* which showed no increase in Ca in live tissue, contains less structural material than the graminoid species (Odum and Heywood 1978). Calcium concentrations in *Cladium* were greater one year after fire than immediately postburn (Steward and Ornes 1975), but in *Aristida stricta* levels were high immediately postburn and then declined (Christensen 1977).

Magnesium increased in soils of both burned marshes after fire (Schmalzer and Hinkle 1992). Species differed in their response one year after fire with *Juncus* declining in tissue concentration, while concentrations in *Spartina* and *Sagittaria* increased. Relative proportions also changed; Ca was more abundant relative to Mg in *Juncus* but less abundant in *Spartina* and *Sagittaria* one year after fire. Species may differ in their uptake and allocation of nutrients, although the availability of all cations increased after fire.

Wetland plants exhibit a wide range of nutrient concentrations that vary with species, site, plant part, and tissue age (Boyd 1978). Preburn N concentrations for live *Juncus roemerianus* here are within, although at the low end of, the range for that species (Table 6). Nitrogen levels one year postburn are lower than other data. Phosphorus concentrations preburn and one year postburn are within but at the low end of the reported range; K levels are low compared to other data (Table 6). Preburn Ca concentrations are about in the middle of reported values, while levels one year after fire are at the upper range of reported values (Table 6). Magnesium levels are low compared to other data (Table 6).

Previous reports of *Spartina bakeri* nutrient concentrations are not known. It appears to be consistently lower in nutrients than *Spartina alterniflora* Loisel. or *Spartina cynosuroides* (Table 6). Nitrogen levels reported for *Spartina spartinae* range from 0.62 to 1.12% (McAtee et al. 1979a), also exceeding *Spartina bakeri*. Phosphorus levels in *Sagittaria lancifolia* L. are lower than in *Sagittaria*

Table 6. Nutrient concentrations in *Juncus roemerianus*, *Spartina bakeri*, and related marshes

Biomass Type	Location	Nutrient Concentration (%)					Reference
		N	P	K	Ca	Mg	
Juncus roemerianus young	Mississippi	0.96	0.19	—	—	—	de la Cruz and Gabriel (1974)
Juncus roemerianus mature	Mississippi	0.78	0.14	—	—	—	de la Cruz and Gabriel (1974)
Juncus roemerianus unburned, regrowth	Mississippi	1.04	0.119	1.68	0.027	0.134	Faulkner and de la Cruz (1982)
Juncus roemerianus burned, regrowth	Mississippi	1.75	0.260	2.10	0.061	0.198	Faulkner and de la Cruz (1982)
Juncus roemerianus seasonal range	Georgia	0.7–1.0	0.13–0.15	1.0–1.2	0.04–0.10	0.09–0.12	Gallagher et al. (1980)
Juncus roemerianus live	Florida	0.91–1.02	0.04	1.01–1.06	<0.01–0.02	0.12–0.16	Kruczynski et al. (1978)
Juncus roemerianus live, preburn	Florida	0.73	0.060	0.547	0.056	0.052	This study
Juncus roemerianus live, 1 yr postburn	Florida	0.39	0.046	0.432	0.115	0.042	This study
Juncus roemerianus standing dead	Mississippi	0.62	0.13	—	—	—	de la Cruz and Gabriel (1974)
Juncus roemerianus dead	Florida	0.50–0.62	0.01–0.02	0.37	0.03–0.06	0.12–0.19	Kruczynski et al. (1978)
Juncus roemerianus dead, preburn	Florida	0.54	0.034	0.100	0.171	0.052	This study
Juncus roemerianus dead, 1 yr postburn	Florida	0.24	0.023	0.055	0.204	0.041	This study

Table 6. Continued

Biomass Type	Location	Nutrient Concentration (%)					Reference
		N	P	K	Ca	Mg	
Spartina cynosuroides unburned, regrowth	Mississippi	1.48	0.214	2.080	0.116	0.234	Faulkner and de la Cruz (1982)
Spartina cynosuroides burned, regrowth	Mississippi	1.63	0.230	2.011	0.102	0.203	Faulkner and de la Cruz (1982)
Spartina alterniflora live, range of studies	Various	0.7–1.7	0.08–0.20	0.78–1.43	0.15–0.30	0.24–0.46	Ornes and Kaplan (1989)
Spartina bakeri live, preburn	Florida	0.30	0.018	0.315	0.064	0.030	This study
Spartina bakeri live, 1 yr postburn	Florida	0.18	0.030	0.438	0.134	0.074	This study
Spartina bakeri dead, preburn	Florida	0.39	0.011	0.060	0.094	0.025	This study
Spartina bakeri dead, 1 yr postburn	Florida	0.14	0.010	0.023	0.139	0.036	This study
Sagittaria latifolia live	South Carolina	—	0.58	3.20	1.42	0.20	Garten (1978)
Sagittaria latifolia live	South Carolina	—	0.30	4.04	0.55	0.18	Boyd (1978)
Sagittaria lancifolia live, preburn	Florida	1.51–1.73	0.105–0.153	3.30–3.35	0.49–0.52	0.22–0.26	This study
Sagittaria lancifolia live, 1 yr postburn	Florida	0.69–0.71	0.096–0.110	2.22–2.47	0.50–0.52	0.26–0.31	This study

latifolia Willd. Potassium levels preburn are within range and those postburn somewhat lower compared to other data. Calcium levels are slightly lower, and Mg slightly higher than other data (Table 6).

Species that resprout after fire may alter nutrient uptake rates, tissue nutrient concentrations, growth rates, leaf turnover, and photosynthesis since they must adapt to a wide range of environmental conditions (Chapin and Van Cleve 1981). At least some of these changes appear to occur in these resprouting marsh species.

Nutrient concentrations in live and dead biomass followed expected patterns. Live biomass was higher in N, P, and K which are readily lost from senescent or dead tissue (Tukey 1970, de la Cruz and Gabriel 1974, Kruczynski et al. 1978, Marschner 1986); remobilization and reabsorption of mobile elements from senescent tissue also occurs in some species (van der Linden 1980, Marschner 1986, Bernard et al. 1988). Magnesium also generally declined from live to dead biomass; leaching probably occurred (Tukey 1970). Standing dead biomass was high in Ca, some of which is leached from leaves (Tukey 1970), but that incorporated in structural material is not as readily lost (Tukey 1970, Epstein 1972), and it is not remobilized and reabsorbed from senescent leaves (Marschner 1986).

Decomposition rates of standing dead *Juncus roemerianus* stems are low (Christian et al. 1990), and stems may require eight years to decompose where not removed by tidal action or fire (Eleuterius and Lanning 1987). Decomposition rates of standing *Spartina bakeri* are unknown, but it also probably requires several years. In contrast, *Sagittaria lancifolia* probably decomposes much more rapidly, similar to *Sagittaria latifolia* (Odum and Heywood 1978). However, the standing dead material that was present one year after fire was largely material that had been produced since the fire and then died; most partially burned residue was not evident after one year (P. Schmalzer, pers. obs.). This accounts for the frequently parallel changes in nutrient concentrations in live and dead biomass one year after fire. For example, the decreased N levels in standing dead biomass and the increased Ca in dead *Juncus* and *Spartina* one year postburn reflect the changes in the live tissue from which they were derived.

Nutrient Standing Crops

Nutrient standing crops in the *Juncus* marsh before burning are within the range reported for similar marshes, while those one year postburn are low (Table 7). Previous data on *Spartina bakeri* marshes are not known, but their standing crops before burning are similar to *Juncus*, *Spartina cynosuroides*, and *Cladium jamaicense* marshes (Table 7).

Nutrient standing crops change as a consequence of changes in biomass and in nutrient concentrations. All biomass categories were much lower one year after fire then preburn. The proportions of biomass categories changed; standing dead recovered less of its preburn biomass than live in one year (Schmalzer et al. 1991b). Where concentrations all decreased (e.g., N), nutrient standing crops declined more than biomass. Even where concentrations increased (Ca), total standing crops were still lower than preburn due to the biomass changes. Nutrient standing crops recovered less in one year after fire in our *Juncus* and *Spartina*

Table 7. **Nutrient standing crops in *Juncus roemerianus*, *Spartina bakeri*, and related marshes**

Biomass Type	Location	Nutrient Standing Crop (g/m^2)					Reference
		N	P	K	Ca	Mg	
Juncus roemerianus seasonal range	Georgia	6–10	1.0–1.8	7–14	5–10	0.6–1.2	Gallagher et al. (1980)
Juncus roemerianus preburn	Mississippi	8.76	0.22	3.88	1.44	1.94	Faulkner and de la Cruz (1982)
Juncus roemerianus preburn	Florida	12.92	0.94	8.86	3.47	1.38	This study
Juncus roemerianus 1 yr postburn	Florida	1.94	0.22	2.24	1.16	0.38	This study
Spartina cynosuroides preburn	Mississippi	7.25	0.29	3.70	0.88	1.04	Faulkner and de la Cruz (1982)
Spartina bakeri preburn	Florida	10.24	0.38	7.07	3.30	1.00	This study
Spartina bakeri 1 yr postburn	Florida	1.12	0.13	1.62	0.89	0.33	This study
Cladium jamaicense mature	Florida	5.5–8.9	0.25	6.5	3.3	5.8	Steward and Ornes (1975)
Cladium jamaicense 1 yr postburn	Florida	4.8	0.18	3.8	3.1	4.6	Steward and Ornes (1975)

marshes than in a *Cladium* marsh (Stewart and Ornes 1975) even though biomass recovery (Schmalzer et al. 1991b) was similar.

Nutrient Cycling Considerations

Wetlands fires can result in substantial losses of N from above-ground biomass (van der Linden 1980, Faulkner and de la Cruz 1982) with smaller losses of K and redistribution of less volatile elements (Faulkner and de la Cruz 1982). Above-ground standing crops of biomass and nutrients in our marshes require more than one year to recover. Below-ground biomass, roots and rhizomes, in *Juncus roemerianus* greatly exceeds (4–5 ×) above-ground (de la Cruz and Hackney 1977). This is probably true in *Spartina bakeri* but data are lacking. Changes in below-ground biomass and its nutrient concentrations after fire are unknown. These may buffer losses from the above-ground system but quantification is needed. Nitrogen recirculated from rhizomes to shoots in *Phragmites australis* Trin. was estimated at 25–50% (van der Linden 1980). Nutrient recirculation is important in some *Carex* wetlands (Bernard and Solsky 1977, Bernard et al. 1988).

CONCLUSIONS

Fire had substantial effects on nutrient concentrations and standing crops in these marshes that require more than one year to return to preburn conditions. Since available soil N did not increase until six months after fire in these sites that were flooded at the time of burning (Schmalzer and Hinkle 1992), limitations on available N may have affected tissue N levels, although N deficiencies were not evident. Species responded differently to the increased availability of nutrients after fire. *Juncus* and *Spartina* both accumulated calcium but *Sagittaria* did not; *Spartina* accumulated magnesium but *Juncus* did not. Changes in nutrient concentrations and standing crops in below-ground biomass after fire need to be investigated to determine whether these buffer changes in the above-ground system. A time series of biomass samples after fire would be useful in determining whether regrowth immediately after fire showed elevated nutrient levels, and how nutrient levels changed with time since fire.

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